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NEW FOSSIL LEPORIDAE FROM MONGOLIA[1]

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The fossil Leporidae described in the following pages are represented in the collections of The American Museum of Natural History made by the Central Asiatic Expeditions under the leadership of Dr. Roy Chapman Andrews. It has been the privilege of the author to study and to describe this material from the Eocene and the Oligocene of Mongolia through the courtesy of Dr. Walter Granger and the authorities of The American Museum of Natural History. The illustrations for this article are taken from the drawings of Mr. Sydney Prentice. The present study, carried out in the Graduate School of Duquesne University, was made possible by the writer's tenure of a Thornton Fellowship in Scientific Research.

ORDER DUPLICIDENTATA (LAGOMORPHA)

LEPORIDAE GRAY

Mytonolaginae, new subfamily

Lagomorphs with tooth formula of I_1^2 C_0^0 P_2^3 M_3^3; cheek teeth with roots and without cement. Terminal members of cheek tooth series functional. P^2 approximating M^3 in size; M_3 approximating P_3 or P_4. M_1 the largest and most transverse of the superior cheek teeth; M_2 the largest and most transverse of the inferior cheek teeth. P_3 trilobate, with one external and two internal reëntrants, its anterior lobe without grooves or furrows on its anterior face.

INCLUDED GENERA.—*Mytonolagus*, *Shamolagus*, new genus, and *Gobiolagus*, new genus.

KNOWN RANGE.—Upper Eocene, North America and Asia, Lower Oligocene, Asia.

SHAMOLAGUS,[2] NEW GENUS

GENOHOLOTYPE.—*Shamolagus grangeri*, new species.

DIAGNOSIS.—A genus nearly related to *Mytonolagus*, but less progressive in specialization; M_2 considerably exceeding M_1 in size, M_3 approximating P_4 in size. Lateral slopes of cheek teeth not as steep as in *Mytonolagus*. Protoconids of P_4 and M_1 tapering to the occlusal surface but showing hypertrophy and inflation toward the base of the crown.

Shamolagus grangeri,[3] new species

Figure 1

HOLOTYPE.—A.M.N.H. No. 26289, a left mandibular ramus with P_4, M_{1-3}, incisor lost.

HORIZON.—Ulan Shireh, Upper Eocene. Irdin Manha Beds.

LOCALITY.—Chimney Butte, North Mesa, Shara Murun Region, Inner Mongolia. Central Asiatic Exped., 1928.

DIAGNOSIS.—A smaller species than *Mytonolagus petersoni*, mandible more slender, of lighter construction throughout and narrowing anteriorly in front of M_2. P_4 and M_1 apparently lower-crowned than in *Mytonolagus petersoni*, M_3 large, functional, with prominent third lobe.

In comparison with *Mytonolagus petersoni* of the North American Eocene, the present species is smaller, while the mandibular ramus is more slender and lighter. The diastema appears to have had nearly the same relative extent in both forms. The ramus of *Shamolagus grangeri* does not show the anterior depth of *Mytonolagus petersoni*, anteriorly the transverse narrowing of the ramus occurs just in advance of M_2, whereas in the American species this narrowing begins just in advance of M_1. The anterior mental foramen is located well in advance of P_3 in *Shamolagus grangeri* but is posterior to the mid-point of the diastema. A posterior mental foramen is

[1] Publications of the Asiatic Expeditions of The American Museum of Natural History, Contribution No. 143.

[2] From the Chinese Sha-mo—"sand desert," an old name for the Gobi, and the Greek λαγώς—hare.

[3] The specific name is in honor of Dr. Walter Granger.

found beneath the anterior root of M_1, posterior to its place in *Mytonolagus petersoni*. The slope of the ascending ramus is definitely lower than in *Palaeolagus* and in most species of *Desmatolagus*. There is a fairly shallow masseteric fossa, the inferior border of which is rounded, not sharp; anteriorly the ridge-like scar becomes a relatively large boss-like tubercle, larger than I have noted this structure in any other duplicidentate species. Between the tubercle and the ascending wing of the ramus there is an area where the anterior border of the fossa is poorly defined, but its limits are sharply shown in relation to the ascending ramus. Beyond the fact that it is quite shallow and does not contain the foramen posterior to M_3, but it is still a fair-sized tooth, functional, and with a prominent third lobe. The largest tooth in the row is M_2; the increase in size initiated here has not yet affected M_1 and the premolars to a comparable degree.

Although P_3 is lost, its alveoli indicate a tooth the base of which narrowed anteriorly. Apparently P_3 had a greater antero-posterior extent than P_4, and was a little less transverse posteriorly. It seems to have been double-rooted, the roots arranged antero-posteriorly.

Judging from the relatively more transverse P_4 of *Shamolagus grangeri* and the gentler slope of its protomere walls when the tooth is compared with P_4 of *Mytonolagus petersoni*, that tooth in the Mongolian species was lower-crowned than P_4 of the American form. The molars of *Shamolagus grangeri*, with the exception of M_3, were probably lower-crowned as well. In other respects P_4 of the present species differs rather sharply from the corresponding premolar in *Mytonolagus petersoni*. On the buccal side the trigonid wall expands rapidly toward the base, swelling out externally and posteriorly and crowding the talonid wall, which in turn narrows rootward. In P_4 of *Mytonolagus petersoni* there is not the marked external projection of the trigonid at the antero-external angle; there is less swelling of the trigonid wall and the talonid wall narrows less rapidly below. Also, in the Uinta Eocene form, the transition from crown to root on

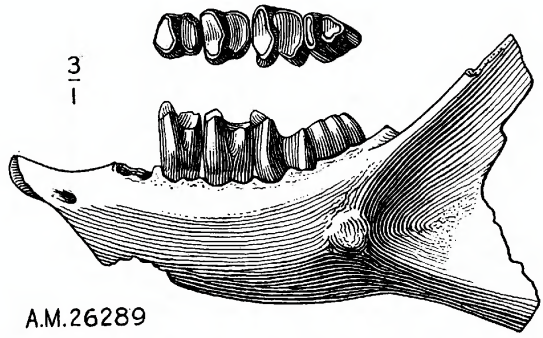

Fig. 1. *Shamolagus grangeri* Burke, holotype, A.M.N.H. No. 26289. Lateral view of mandibular ramus and occlusal view of P_4, M_{1-3} left, ×3.

the *sulcus ascendens* appears of the leporine type, and what is preserved of the plate representing the coronoid would indicate that the latter process was already well reduced in Upper Eocene lagomorphs. The dental foramen is large and slit-like, and obliquely directed, in contrast with its nearly vertical direction in *Palaeolagus*.

None of the incisor is preserved, and it is difficult to trace its former extent, but it is probable that it took its origin beneath M_2.

The cheek teeth of the holotype contrast strongly with those of more recent lagomorphs. They are low-crowned, rooted, without cement, and, in proportion to the slender ramus, large and transverse. The reduction of M_3 has begun,

the protomere is not indicated by any abrupt expansion of the crown, whereas in *Shamolagus grangeri* there is a decided buccal inflation of the tooth above the root. In occlusal section the trigonid of P_4 of *Shamolagus grangeri* has more of a pear-shape than that of *Mytonolagus petersoni*.

The "third lobe" of P_4 of *Shamolagus grangeri* is indicated by a notch at the postero-internal angle of the talonid. The implantation of the tooth is essentially as in *Mytonolagus petersoni*. There are two roots, antero-posteriorly arranged; the anterior root is compressed fore and aft.

In *Shamolagus grangeri* M_1 is a larger tooth than in P_4 and differs from the latter in the greater antero-posterior compression of its trigonid on the buccal side; this gives the trigonid a narrower occlusal section on the protomere and makes for a wider external valley in the tooth. From M_1 of *Mytonolagus petersoni* this tooth differs in showing gentler buccal wall slopes, greater projection at the antero-external angle, and more abrupt expansion of the crown wall above the roots. The talonid of M_1 of *Shamolagus grangeri* is larger, relative to the trigonid, than is the talonid of P_4; it is also larger, in this respect, than in M_1 of *Mytonolagus petersoni*. In M_1 of the Gobi species, as also in P_4, the lingual reëntrant is quite persistent, reaching well toward the base of the crown, as in the Uinta species. The two roots are arranged antero-posteriorly.

As mentioned above, M_2 is the largest of the cheek teeth, exceeding M_1 in both transverse and antero-posterior dimensions. The buccal wall of the trigonid is more compressed antero-posteriorly and is bent anteriorly; the anterior face of the trigonid bears a distinct groove on its protomere side. The external valley is wider than in M_1 and the talonid larger. Compared with M_2 of *Mytonolagus petersoni* the tooth shows greater extension and compression of the protomere wall of the trigonid, with the antero-external angle of the crown produced much farther bucally; there is a more prominent groove on the protomere side of the anterior face of the trigonid, while the external valley is wider and the talonid larger, relatively, than in the Uinta Eocene species. A further difference is to be found in the roots of M_2 in the two forms; in *Shamolagus grangeri* the anterior and the posterior roots are separated; they are conjoined in *Mytonolagus petersoni*.

In size, M_3 approaches P_4 and is a larger tooth than the last molar in *Mytonolagus petersoni*. It shows more extension antero-posteriorly than M_3 of the American Eocene species and has a prominent talonid; there is, in addition to the main buccal valley, a postero-external valley marking off a large "third lobe." The internal valley is still indicated. The entire crown has not yet appeared above the alveolar wall in the holotype; the tooth appears to have been fully as high crowned as M_3 in *Mytonolagus petersoni*.

MEASUREMENTS

Shamolagus grangeri Burke, A.M.N.H. No. 26289 (holotype)

	mm.
P_3 antero-posterior, at alveolus	2.3
P_3 transverse, at alveolus	1.3
P_4 antero-posterior (occlusal surface)	1.9
P_4 transverse (occlusal surface)	1.6
P_4 transverse (at alveolus)	1.9
M_1 antero-posterior (occlusal surface)	2.0
M_1 transverse (occlusal surface)	2.1
M_1 transverse (at alveolus)	2.1
M_2 antero-posterior (occlusal surface)	2.3
M_2 transverse (occlusal surface)	2.3
M_2 transverse (at alveolus)	2.6
M_3 antero-posterior (occlusal surface)	1.8
M_3 transverse (occlusal surface)	1.5
M_3 transverse (at alveolus)	1.7
Length of inferior premolar series at alveoli (app.)	3.9
Length of inferior molar series (occlusal surface)	6.2
Length of inferior molar series (at alveoli)	7.6
Length mandibular tooth row at alveoli (app.)	10.7
Depth ramus under M_1 (lingual side)	6.9
Width superior region of ramus below M_2	3.5
Width superior region of ramus below M_1	3.1
Width superior region of ramus below P_4	2.6
Width superior region of ramus below P_3	2.2
Diastema between inferior I and P_3	5.8

Shamolagus medius,[1] new species

Figure 2

HOLOTYPE.—A.M.N.H. No. 26144, the anterior portion of a right mandibular ramus with broken incisor and P_{3-4}, M_1.

[1] The specific name is suggestive of its intermediate position between species of *Desmatolagus* and *Shamolagus*.

HORIZON.—Shara Murun, Upper Eocene.

LOCALITY.—Near Baron Sog, Inner Mongolia. Central Asiatic Exped., 1925.

DIAGNOSIS.—Near *Shamolagus grangeri* in size. Crown of P_3 trilobate at occlusal surface, with one external and two internal reëntrants; anterior lobe sub-round in occlusal section, not compressed or grooved anteriorly. External valleys of P_4 and M_1 wider than in *Shamolagus grangeri;* talonid of P_4 more reduced, talonid of M_1 more triangular and trigonid of M_1 more compressed antero-posteriorly along the protomere.

The anterior part of the ramus which constitutes the holotype does not display any marked departures from that of *Shamolagus grangeri,* except that it shows somewhat greater fullness in the region of P_4 and M_1, and its outline below these teeth suggests less expansion below M_2 than is found in the latter species. The two forms

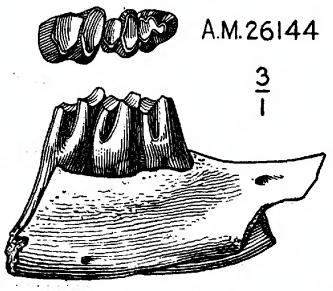

Fig. 2. *Shamolagus medius* Burke, holotype, A.M.N.H. No. 26144. Lateral view of the partial mandibular ramus and occlusal view of P_{3-4}, M_1 right, ×3.

are nearly the same in size and correspond fairly well in length of diastema. In *Shamolagus medius* both mental foramina are preserved; the anterior mental foramen has a more anterior position and is higher on the ramus than in *Shamolagus grangeri.*

The inferior incisor is flattened, or only slightly rounded anteriorly and extends posteriorly alongside the roots of M_1; it may have reached alongside the roots of M_2.

Fortunately, P_3 is preserved in this specimen and is not badly worn. If the alveoli for P_3 of the holotype of *Shamolagus grangeri* can be depended upon as indicative of the antero-posterior dimensions of that tooth, the P_3 of *Shamolagus medius* is reduced in comparison with P_3 of the genotypic species. This tooth, as preserved in the holotype, shows three reëntrants, one external and two internal. The external reëntrant is the most transverse and persistent; together with the antero-internal reëntrant, which occurs well in advance of it, it delimits the prominent anterior lobe of the tooth. The anterior lobe is attenuated from below to the occlusal surface, particularly on the anterior and buccal sides, sub-round in occlusal section and apparently represents the trigonid. The lobe shows no definite evidence of flattening or grooving on the anterior face at this stage of wear.

The postero-internal reëntrant occurs a little posterior to the external reëntrant. It is less persistent than the antero-internal reëntrant and has less transverse extent across the crown. The posterior wall of the talonid is flattened and compressed against the anterior face of P_4; the protomere pillar of the talonid is attenuated from the base upward. The tooth is strongly produced laterally at the postero-external angle. The enamel of P_3 is carried well down the anterior root.

In the holotype of *Mytonolagus petersoni* P_3 is too worn to furnish adequate comparison with this premolar in *Shamolagus medius.* However, P_3 of the Uinta Eocene species appears to have had steeper lateral and medial walls; the anterior lobe was relatively larger and the base of the crown was not produced laterally beyond the anterior lobe at the postero-external angle of the tooth.

From the corresponding tooth in *Shamolagus grangeri* P_4 differs in having a wider external valley, in showing a less swollen crown base, and in having the talonid reduced. In some respects the tooth shows an approach to P_4 of *Mytonolagus petersoni,* but P_4 of the Uinta Eocene species shows steeper lateral slopes, less inflation of the base of the trigonid, the inflation of the lateral crown base above the root is generally less marked, and the antero-external angle of the tooth is not produced laterally to such an extent. P_4 of the holotype of *Shamolagus medius* still shows a trace of the postero-internal reëntrant.

The M_1 of *Shamolagus medius* shows a

wider external valley, greater antero-posterior compression of the lateral side of the trigonid, and less inflation of the crown base at the antero-external angle of the tooth than does M_1 of *Shamolagus grangeri*. The talonid is also larger and more triangular in the Shara Murun species. It is distinguished from M_1 of *Mytonolagus petersoni* by the same characters that differentiate P_4 in the two species.

exposure, P_4 and molars showing strong lateral hypertrophy of trigonids, M_{1-2} predominating over other mandibular cheek teeth in size. P_3 with modified *Shamolagus* pattern.

Gobiolagus tolmachovi,[1] new species

Figure 3

HOLOTYPE.—A.M.N.H. No. 26142, a left mandibular ramus with all the cheek teeth and a broken incisor.

REFERRED SPECIMEN.—A.M.N.H. No. 26143,

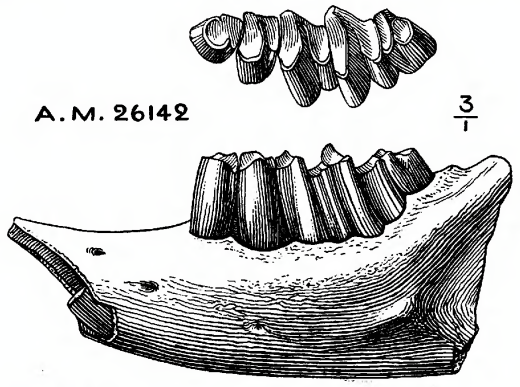

Fig. 3. *Gobiolagus tolmachovi* Burke, holotype, A.M.N.H. No. 26142. Lateral view of mandibular ramus and occlusal view of P_{3-4}, M_{1-3} left, ×3.

MEASUREMENTS

Shamolagus medius Burke, A.M.N.H. No. 26144 (holotype)

	mm.
P_3 antero-posterior (occlusal surface)	1.5
P_3 transverse (occlusal surface)	1.2
P_3 transverse (at alveolus)	1.3
P_4 antero-posterior (occlusal surface)	1.7
P_4 transverse (occlusal surface)	1.7
P_4 transverse (at alveolus)	2.0
M_1 antero-posterior (occlusal surface)	2.2
M_1 transverse (occlusal surface)	2.2
M_1 transverse (at alveolus)	2.1
Length of inferior premolar series at alveoli	3.4
Length of inferior premolar series at occlusal surface	2.8
Width superior region of ramus below M_1	3.2
Width superior region of ramus below P_4	2.8
Width superior region of ramus below P_3	2.0
Diastema between inferior I and P_3	5.5
Inferior I antero-posterior	1.5
Inferior I transverse	1.5

GOBIOLAGUS, NEW GENUS

GENOHOLOTYPE.—*Gobiolagus tolmachovi*, new species.

DIAGNOSIS.—Related to *Mytonolagus* and *Shamolagus*, but distinguished by marked unilateral hypsodonty and non-persistence of the internal valleys of the cheek teeth; talonid of P_4 reduced; talonids of P_{3-4} with slight lateral

a fragmentary left mandibular ramus preserving P_4, M_{1-2} in shattered state. Anterior region of ramus missing.

HORIZON.—Shara Murun, Upper Eocene.

LOCALITY.—Near Baron Sog, Inner Mongolia. Central Asiatic Exped., 1925.

DIAGNOSIS.—Cheek teeth more hypsodont than in any other known Eocene duplicidentate; P_3 with main internal reëntrant well in advance of external reëntrant, as in *Shamolagus*. M_3 approaching P_4 in occlusal dimensions, but much less hypsodont. M_1 with somewhat, P_4 with definite pear-shaped occlusal section of trigonid. Talonid of P_4 weak. P_{3-4} characterized by slight lateral exposure of talonids, strong trigonids, groove-like external reëntrants.

The mandibular ramus of the holotype indicates a species smaller than *Mytonolagus petersoni* but approaching *Shamolagus grangeri* in size. In depth (particularly in the anterior region) and in heaviness, the ramus falls short of that of the American form, but exceeds that in the species of *Shamolagus* in these respects. The diastema is somewhat greater than in *Shamolagus* and in *Mytonolagus*. The

[1] The specific name is given in honor of Dr. I. P. Tolmachoff.

ramus narrows transversely anterior to M_1. In the holotype specimen there are two anterior mental foramina; the most anterior of the two is carried farther forward than in *Shamolagus medius*, while the posterior one occurs between the latter and P_3, but lower on the ramus. The posterior mental foramen occurs under P_4. The slope of the ascending ramus is steeper than in *Shamolagus grangeri*, the masseteric fossa is moderate, with better definition of the superior border than in the holotype of *Shamolagus grangeri*. The tubercle marking the apex of the fossa anteriorly is prominent but not comparable with the boss-like tubercle found there in *Shamolagus grangeri*. The dental foramen seems to have had more of a vertical direction than that of the latter species.

The mandibular incisor is triangular in transverse section, with the apex of the triangle posterior. Its anterior face is flattened or only a little rounded. The incisor was carried back under M_2, as indicated by the incisive swelling.

The outstanding feature of the cheek teeth of *Gobiolagus* is hypsodonty, which quickly distinguishes them from those of *Shamolagus*. In this respect also they go beyond *Mytonolagus*. The hypsodonty is of the unilateral type, with the enamel carried well down the shaft on the lateral side; correlated with it is non-persistence of the internal valleys, which disappear after moderate wear. These features have their effect on the tooth pattern, and in particular on that of P_3, but not enough to conceal its ultimate origin from a pattern which must have been much like that of P_3 of *Shamolagus medius*.

Another character of these teeth has its origin in hypertropic development of the lateral side of the trigonids. This tendency has been mentioned in the case of *Shamolagus*, but it should be indicated that in *Mytonolagus* also, particularly in the premolars, the base of the trigonid shaft shows some hypertrophy. It may be that early lagomorph cheek teeth in general showed something of this tendency, but in *Shamolagus* and in *Gobiolagus* it is quite marked. In these forms we trace, first, marked inflation of the lateral base of the trigonid; in a later sequence there follows antero-posterior compression of the trigonid shaft on the lateral side, which causes this element of the crown to jut laterally and out of proportion to the rest of the tooth.

The anterior cheek teeth of *Gobiolagus tolmachovi* are still in the first stage—that of hypertrophy of the lateral side of the trigonid. The posterior cheek teeth, on the other hand, have undergone the antero-posterior compression of the trigonid and show it jutting laterad.

The unique type of tooth row found in *Gobiolagus*, then, appears to be the result of a combination of two growth factors: hypertrophy of the lateral trigonid walls—a characteristic which *Gobiolagus* shares with *Desmatolagus* and to a lesser degree with *Mytonolagus*—and precocious (in a phylogenetic sense) unilateral hypsodonty. (Antero-posterior compression of the protomere walls is no unique feature, but appears to occur in all lagomorph lines.) Further individuality of the tooth row is due to a third factor, atrophy, displayed by the talonids of the premolars.

The P_3 of this species arises as a stout shaft, like a cylinder compressed transversely. In lateral view the cylindrical appearance is particularly striking. Postero-laterally the external reëntrant is found; in the present specimen it extends but half the height from the occlusal surface to the alveolar border, and is in any case quite narrow and slit-like, extending a little more than a third of the distance across the crown surface at the present stage of wear.

On the median side is found the last trace of the antero-internal reëntrant, here carried well in advance of the external reentrant. The two reëntrants divide the crown into two lobes, an anterior, subround trigonid, without additional reentrants, and a posterior triangular talonid, which probably, at an earlier stage of wear, retained a postero-internal reentrant. The talonid shows little exposure on the lateral side—merely the apex of the triangle appears at the postero-lateral angle of the crown—but its median exposure exceeds that of the trigonid. The

tooth shows marked unilateral hypsodonty; the enamel extends down the lateral side beneath the alveolar border in the holotype specimen: on the median side of the crown the enamel descends more than half the height of the crown and is most persistent anteriorly.

The pattern is plainly a derivative of the type found in *Shamolagus medius*. There is no evidence of any division of the anterior lobe, and the deviations from the *Shamolagus* pattern shown in P_3 of the holotype of *Gobiolagus tolmachovi* are plainly due to the peculiar effects of progressive unilateral hypsodonty.

The P_4 of this species is a distinctive tooth. It shows the features of P_4 in the *Gobiolagus* line (hypertropic growth of the trigonid and a weak talonid) but at the same time retains characters relating it to *Shamolagus*. The outjutting trigonid of this form is simply an exaggeration of the basal inflation of the trigonid seen in P_3 of *Shamolagus*, emphasized in the process of hypsodonty. The pear shape of the occlusal surface is a feature also found in P_4 of *Shamolagus*. What is distinctly a *Gobiolagus* character, however, is the slight development of the talonid, which appears compressed between the trigonids of P_4 and M_1 and has such a slight lateral exposure as to make the lateral side of the trigonid of P_4 appear the only functional part of the protomere of the tooth. To my knowledge this is the most distinctive feature of the *Gobiolagus* line—the diminutive size of the talonid of P_4.

Among other characters of P_4 of this species which should be emphasized are the non-persistence of the internal valley and some median projection of the trigonid beyond the talonid. In A.M.N.H. No. 26143 the base of the tooth shaft is preserved; it shows the enamel extending down the lateral side of the shaft at a sharp angle. The tooth is rooted, and grooves would indicate that there are two roots, antero-posteriorly arranged.

The molars of this species resemble P_4 in that they show the hypertrophy of the trigonid and the lack of persistence of the internal valley, together with unilateral hypsodonty. The protomere sides of the molar trigonids are not robust and rounded in section, however, but have undergone antero-posterior compression and jut laterad. Mediad they also project beyond the talonids to a degree. None of the talonids are of the diminutive type found in P_4.

The M_1 of *Gobiolagus tolmachovi* somewhat resembles P_4 in preserving the pear-shaped occlusal section found in the latter. The trigonid has undergone antero-posterior compression to a much greater degree than in the latter tooth, though, and projects far lateral to the talonid. It is interesting to find that the pear-shaped occlusal section in M_1 of this species is more marked than in M_1 of *Shamolagus*. Although the talonid of M_1 of *Gobiolagus tolmachovi* is small, relative to the wide trigonid, it is not of the reduced type found in P_4, and the external valley is wider. The discrepancy in size between P_4 and M_1 is marked, the molar is well in excess of the premolar in size.

The largest tooth in the row, as in *Mytonolaginae* generally, is M_2, although it is not greatly in excess of M_1 in this case. Unlike the latter, the trigonid occlusal section has lost the pear shape and the protomere side of the trigonid is compressed antero-posteriorly. The external valley is wider than in M_1. As in M_1, the trigonid juts out laterally to a marked degree. My specimens do not show the number of roots in this tooth.

The M_3 of this species is smaller, in comparison with M_{1-2}, than in *Shamolagus grangeri* and *Mytonolagus petersoni*. Its trigonid is compressed antero-posteriorly, as is that of *Shamolagus grangeri*, but the talonid is sub-round in occlusal section. The M_3 of the holotype shows both the internal and the external reëntrant valleys, but no trace of the "third lobe."

MEASUREMENTS

Gobiolagus tolmachovi Burke, A.M.N.H. No. 26142 (holotype)

	mm.
Inferior I, antero-posterior	1.5
Inferior I, transverse	1.3
P_3 antero-posterior (occlusal surface)	1.4
P_3 transverse (occlusal surface)	1.3
P_4 antero-posterior (occlusal surface)	1.6

P_4 transverse (occlusal surface)	1.9
M_1 antero-posterior (occlusal surface)	2.0
M_1 transverse (occlusal surface)	2.5
M_2 antero-posterior (occlusal surface)	2.1
M_2 transverse (occlusal surface)	2.8
M_3 antero-posterior (occlusal surface)	1.4
M_3 transverse (occlusal surface)	1.8
Length of inferior premolar series at occlusal surface	3.1
Length of inferior premolar series at alveoli	4.5
Length of inferior molar series at occlusal surface	5.5
Length of inferior molar series at alveoli	6.5
Length mandibular cheek teeth at occlusal surface	8.8
Length mandibular cheek teeth at alveoli	10.1
Depth ramus under M_1 (lingual side)	7.5
Width superior region of ramus below M_2	4.0
Width superior region of ramus below M_1	4.0
Width superior region of ramus below P_4	3.5
Width superior region of ramus below P_3	2.5
Diastema between inferior I and P_3	7.1

A.M.N.H. No. 26097 from Twin Obo, East Mesa, Shara Murun Region, Inner Mongolia. Central Asiatic Exped., 1928.

DIAGNOSIS.—General construction much as in *Gobiolagus tolmachovi*, but P_3 more compressed transversely with main lingual reëntrant more posterior (on worn teeth opposite buccal reëntrant). P_4 somewhat exceeding M_3 in occlusal dimensions. Occlusal sections of P_4 and M_1 not pear-shaped. Protomere walls of cheek teeth steeper, more angular in occlusal section; talonids more transverse. Lateral exposure of talonids of P_{3-4} greater; lateral valleys of P_{3-4} wider.

As a whole, the mandibular ramus of the holotype of *Gobiolagus andrewsi* is larger than that of *Mytonolagus petersoni;* it is also deeper, although the ramus of the American form is relatively heavier. Compared with *Gobiolagus tolmachovi* the ramus

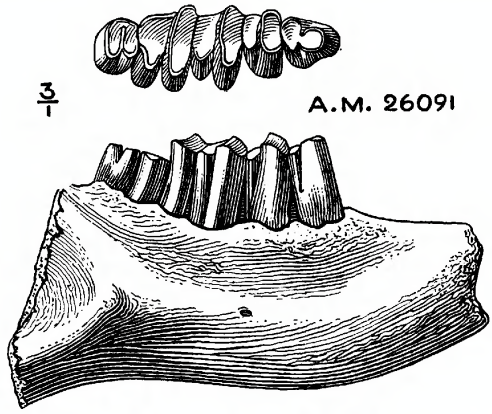

Fig. 4. *Gobiolagus andrewsi* Burke, holotype, A.M.N.H. No. 26091. Lateral view of mandibular ramus and occlusal view of P_{3-4}, M_{1-3} right, ×3.

Gobiolagus andrewsi,[1] new species

Figure 4

HOLOTYPE.—A.M.N.H. No. 26091, a right mandibular ramus with all the cheek teeth and a broken incisor.

REFERRED SPECIMENS.—A.M.N.H. No. 26092, a right mandibular ramus with the incisor and P_{3-4}, M_{1-2}; A.M.N.H. No. 26097, part of right mandibular ramus with the anterior portion missing but retaining a broken incisor, base of P_3 and P_4, and M_{1-3} in place.

HORIZON.—Ulan Gochu, Lower Oligocene.

LOCALITIES.—Holotype, A.M.N.H. No. 26091 and referred specimen A.M.N.H. No. 26092 from Jhama Obo, East Mesa, Shara Murun Region, Inner Mongolia; referred specimen

[1] The specific name is in recognition of the leader of the Central Asiatic Expeditions, Dr. Roy Chapman Andrews.

is larger and deeper, but has about the same heaviness. The diastema is about the same as in *Gobiolagus tolmachovi*. The transverse narrowing of the ramus is abrupt in advance of M_1, an approximation to the condition in *Mytonolagus*. The holotype shows an anterior mental foramen, somewhat atypical, in about the same situation as in *Gobiolagus tolmachovi*. Referred specimen A.M.N.H. No. 26092 shows a typical anterior mental foramen much like the anterior in *Gobiolagus tolmachovi*. The posterior mental foramen is found under P_4. A.M.N.H. No. 26092 shows two posterior mental foramina in this vicinity. The masseteric fossa ap-

pears essentially as in *Gobiolagus tolmachovi*, although the tubercle directly anterior to it does not appear to have been as prominent as in that species.

The incisor of this species appears somewhat less angular than that of *Gobiolagus tolmachovi*, perhaps in this respect resembling that of *Mytonolagus petersoni*. The incisive swelling shows that the tooth took origin under M_2.

In the holotype, P_3 is reminiscent of the same tooth in *Gobiolagus tolmachovi*. The tooth shows greater transverse compression, however, and is elongate antero-posteriorly; the trigonid is attenuated in an anterior direction, the anterior face of the tooth is less rounded. There are two reentrants preserved, as in P_3 of the holotype of *Gobiolagus tolmachovi:* in the holotype of *Gobiolagus andrewsi* both show greater extent across the crown, although they might approximate the condition found in the latter at a later stage of wear. The internal reëntrant appears somewhat more persistent than in *Gobiolagus tolmachovi*. Both reëntrant valleys are wider than those in P_3 of the latter species and are more nearly opposite; in comparison with P_3 of the Shara Murun Eocene species the antero-internal reëntrant appears to have migrated posteriorly while the external reentrant has been carried anteriorly. Relative to the talonid, the trigonid is less prominent than in *Gobiolagus tolmachovi;* the talonid, while still triangular in occlusal view, shows less angularity and a greater lateral exposure. The holotype shows no postero-internal reëntrant, but in A.M.N.H. No. 26092 an unworn P_3 shows it. The distribution of enamel on the shaft is much as in *Gobiolagus tolmachovi;* the tooth is unilaterally hypsodont, the enamel being carried down the shaft beneath the alveolar border on the lateral side, but the dentine is partly exposed on the median side. One specimen, A.M.N.H. No. 26097, preserves the base of the shaft of P_3; the tooth is double-rooted, with the roots arranged antero-posteriorly.

It is of interest, but not necessarily indicative of close relationship, that the pattern of P_3 of this species bears a strong resemblance to that found in P_3 of *Megalagus turgidus* and *Megalagus intermedius*, except that the anterior lobe of the trigonid is not divided. The *Shamolagus* P_3 pattern appears to approximate the primitive pattern of lagomorphs in general.

The P_4 of *Gobiolagus andrewsi* shows specialization beyond that of *Gobiolagus tolmachovi* in the trigonid region. The pear-shaped occlusal section which characterizes the latter species and species of *Shamolagus* is no longer in evidence; in occlusal section the protomere approximates the paramere of the trigonid. This seems to have come about through antero-posterior extension of the trigonid on the paramere, coupled with compression on the protomere. The external valley is wider and the talonid has a greater lateral exposure but it shows little tendency toward an increase in size. A.M.N.H. No. 26097 shows an interruption of the enamel of this tooth on the anterior face toward the base of the shaft. The internal valley is of slight persistence: it appears to have been obliterated in the holotype, but is present in A.M.N.H. Nos. 26097 and 26092.

The molars in *Gobiolagus andrewsi* show greater antero-posterior compression of the trigonids on the protomere; they are in general less transverse with steeper protomere slopes and show relatively larger talonids. The talonids of these teeth have also expanded laterally and the alveolar border is more regular.

The M_1 of this species has lost the pear-shaped occlusal section which characterizes M_1 of *Gobiolagus tolmachovi* and both its trigonids and its talonids are compressed antero-posteriorly on the lateral side. The increase in size of the talonid is most apparent on the protomere. As in *Gobiolagus tolmachovi* this tooth considerably exceeds P_4 in size. A.M.N.H. No. 26097 shows this tooth rooted: apparently the anterior and posterior root canals are conjoined.

As in *Gobiolagus tolmachovi*, M_2 is the largest cheek tooth in the mandibular ramus. The M_2 of the holotype shows a larger talonid than does M_2 of the Shara Murun species, and its talonid shows a reentrant curve at the postero-external angle not shown in M_2 of *Gobiolagus tolmachovi*.

The increase in size of the talonid is most evident in the antero-posterior direction, although in lateral extent the base of the talonid approximates that of the trigonid. The M_2 of A.M.N.H. No. 26097 shows that this tooth is rooted, but while a strong groove appears on the shaft on the buccal side, the anterior and the posterior root canals are conjoined.

While, as in *Gobiolagus tolmachovi*, M_3 in this species is reduced in comparison with M_{1-2}, it is still a functional tooth. It shows a more transverse talonid than that found in M_3 of *Gobiolagus tolmachovi*. The holotype preserves the external valley, but not the internal, and shows indications

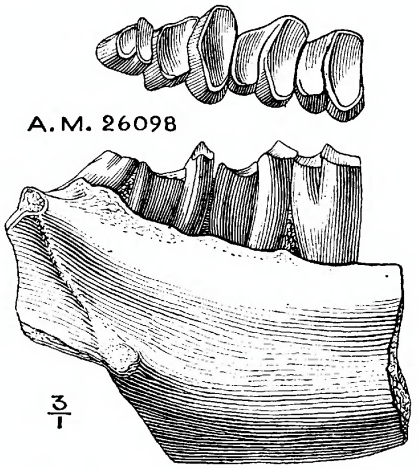

Fig. 5. *Gobiolagus* (?) *major* Burke, holotype, A.M.N.H. No. 26098. Lateral view of partial mandibular ramus and occlusal view of P_4, M_{1-3} right, ×3.

of the "third lobe" toward the base of the crown. A.M.N.H. No. 26097 shows the "third lobe" present as a tiny style on the posterior wall of the tooth, well below the functional occlusal surface of the crown. In A.M.N.H. No. 26097 the tooth is also shown as rooted, with distinct anterior and posterior root canals separated by a common wall.

MEASUREMENTS

Gobiolagus andrewsi Burke, A.M.N.H. No. 26091 (holotype)

	mm.
Inferior I antero-posterior	1.9
Inferior I transverse	2.0
P_3 antero-posterior (occlusal surface)	1.7
P_3 transverse (occlusal surface)	1.3
P_4 antero-posterior (occlusal surface)	1.8
P_4 transverse (occlusal surface)	1.7
M_1 antero-posterior (occlusal surface)	2.0
M_1 transverse (occlusal surface)	2.3
M_2 antero-posterior (occlusal surface)	2.2
M_2 transverse (occlusal surface)	2.5
M_3 antero-posterior (occlusal surface)	1.3
M_3 transverse (occlusal surface)	1.4
Length of inferior premolar series at occlusal surface	2.5
Length of inferior premolar series at alveoli	4.0
Length of molar series at occlusal surface	5.8
Length of molar series at alveoli	6.4
Length of mandibular cheek teeth at occlusal surface	9.1
Length of mandibular cheek teeth at alveoli	10.3
Depth ramus under M_1 (lingual side)	8.3
Width superior region of ramus below M_2	3.9
Width superior region of ramus below M_1	3.5
Width superior region of ramus below P_4	2.9
Width superior region of ramus below P_3	2.0
Diastema between inferior I and P_3	7.0

Gobiolagus (?) **major,** new species

Figure 5

HOLOTYPE.—A.M.N.H. No. 26098, portion of a right mandibular ramus with P_4, M_{1-3} and broken incisor.

HORIZON.—Ulan Gochu, Lower Oligocene.

LOCALITY.—Urtyn Obo, East Mesa, Shara Murun Region, Inner Mongolia. Central Asiatic Exped., 1928.

DIAGNOSIS.—Resembling *Gobiolagus* (?) *teilhardi*, new species, in heaviness of mandibular ramus and reduction of incisor, but a larger species. Cheek teeth much as in *Desmatolagus*, but P_4 of the *Gobiolagus* type.

The mandibular ramus of this species is at once characterized by its relatively great size and heaviness; in these respects it exceeds both *Desmatolagus robustus* and *Gobiolagus* (?) *teilhardi*, new species. The transverse narrowing of the ramus is anterior to M_1; in relative depth the ramus appears nearer *Gobiolagus tolmachovi* but is much heavier. The posterior mental foramen occurs beneath P_4. The superior border of the masseteric fossa is shown sharply defined and rising about as steeply as in *Gobiolagus tolmachovi*. The tubercle anterior to the fossa is strong and boss-like, resembling that in *Shamolagus grangeri* although not as prominent as that in the latter. The dental foramen appears to have been much as in *Gobiolagus tolmachovi*.

The incisor in this form is small, in rela-

tion to the size of the ramus. It is more round, less trihedral than in *Gobiolagus tolmachovi*. This tooth extended back beneath M_1 at least, as indicated by the incisive swelling.

The P_3 is not preserved in the holotype and only specimen.

The P_4 is the most diagnostic tooth in the mandibular ramus; it points to an alliance of this particular species with *Gobiolagus* despite other atypical features of the dentition. The tooth shows atrophy—it is reduced in size in comparison with the molars; the characteristic small talonid of *Gobiolagus*, flattened against the trigonid and without a broad notch at the entrance of the lateral valley, is found here. It is true that the trigonid occlusal section does not have the pear-shape characteristic of the same section in P_4 of *Gobiolagus tolmachovi* but the section is not angular on the lateral side. The trigonid is prominent and appears sub-cylindrical, like a rounded peg, in lateral view, much as in *Gobiolagus andrewsi;* the lateral exposure of the talonid is slight, as in *Gobiolagus* generally. Laterally and medially the trigonid projects beyond the talonid.

Certain features suggest that the molars of this species (M_1 and M_2 at least) are not as advanced in specialization as those of *Gobiolagus tolmachovi* and *Gobiolagus andrewsi*. The ramus of this form is not as deep, indicating a shorter tooth shaft; the enamel of the internal side is persistent, although the teeth are well worn and the internal valley persists in M_1 even at this stage of wear—it shows in conjunction with the external valley in that tooth. These characteristics would indicate that *Gobiolagus* (?) *major* is not only a lower-crowned form than the latter species, but also shows less unilateral hypsodonty in its cheek teeth.

In general, the molars show less antero-posterior compression of the lateral sides of the trigonids than those of *Gobiolagus andrewsi*, thus resembling *Gobiolagus tolmachovi*. Although M_{1-2} are transverse, the trigonids show less lateral expansion than in the same molars in the above species. The trigonids also project mediad beyond the talonids.

The M_2 is the largest cheek tooth in the ramus; its large talonid gives it the excess in size.

The M_3 is much reduced in comparison with M_2; it resembles that of *Gobiolagus tolmachovi* in showing the trigonid larger and more transverse than the somewhat rounded talonid. The tooth is rooted.

The molars of this species are suggestive of those of *Desmatolagus*, but the P_4 is definitely of the *Gobiolagus* type. Further evidence of affinity with *Gobiolagus* may be shown in P_3 when that tooth is known in this form. In the meantime, the evidence furnished by P_4 cannot be overlooked; this type of P_4 is not found in *Shamolagus*, which in every respect seems to stand ancestral to *Desmatolagus*. A further discussion of possible relationships of *Gobiolagus* (?) *major* is given in conjunction with the description of *Gobiolagus* (?) *teilhardi*, new species, which follows.

MEASUREMENTS

Gobiolagus (?) *major* Burke, A.M.N.H. No. 26098 (holotype)

	mm.
Inferior I, antero-posterior	2.3
Inferior I, transverse	2.2
P_4 antero-posterior (occlusal surface)	2.6
P_4 transverse (occlusal surface)	3.3
M_1 antero-posterior (occlusal surface)	3.0
M_1 transverse (occlusal surface)	3.6
M_2 antero-posterior (occlusal surface)	3.1
M_2 transverse (occlusal surface)	3.5
M_3 antero-posterior (occlusal surface)	1.7
M_3 transverse (occlusal surface)	2.0
Length inferior molar series at occlusal surface	7.8
Length inferior molar series at alveoli	8.9
Depth ramus under M_1 (lingual side)	10.7
Width superior region of ramus below M_2	5.0
Width superior region of ramus below M_1	5.0
Width superior region of ramus below P_4	4.7

Gobiolagus (?) teilhardi,[1] new species

Figure 6

Duplicidente indetermine TEILHARD, 1926, Annales de Paleontologie, Tome 15, Fig. 14C, p. 26.

HOLOTYPE.—A.M.N.H. No. 20236, a portion of a left mandibular ramus with broken incisor, base of P_3 and P_4, M_1.

HORIZON.—Hsanda Gol Red Beds, Upper Oligocene.

[1] The species is named for Pierre Teilhard de Chardin, who first described the form but refrained from giving it a specific name.

LOCALITY.—Ten miles west of Loh, Inner Mongolia. Central Asiatic Exped., 1922.

DIAGNOSIS.—Considerably larger than contemporary species of *Desmatolagus;* ramus heavier and deeper. Lateral walls of cheek teeth steeper and P_4 larger, relative to M_1, than in *Gobiolagus andrewsi;* trigonid of P_4 more compressed antero-posteriorly on lateral side and lateral exposure of talonid of P_4 greater, but talonid of reduced type.

The fragmentary mandibular ramus which represents this species in the collection of The American Museum of Natural History indicates a lower jaw which is larger, deeper, and heavier than that of *Desmatolagus robustus*, with which it is

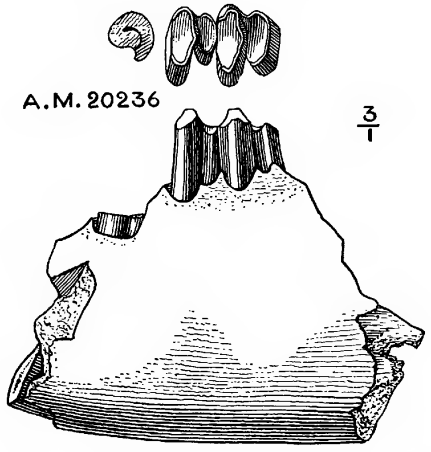

Fig. 6. *Gobiolagus* (?) *teilhardi* Burke, A.M.N.H. No. 20236. Lateral view of portion of mandibular ramus and occlusal view of broken P_3 and P_4, M_1 left, ×3.

associated in the Hsanda Gol fauna. The ramus shows no abrupt transverse narrowing in the vicinity of the anterior cheek teeth. There is a posterior mental foramen beneath and between P_3 and P_4. The mandibular incisor is small, considering the size of the ramus. It shows little curvature on its anterior face and exhibits greater transverse compression than that of *Gobiolagus andrewsi*. The incisive swelling indicates that the tooth arose beneath M_1.

The P_3 of this specimen is broken off at the alveolar border. The transverse section is comma-like, much as the worn occlusal section of the *Megalagus* P_3, but the internal reëntrant cuts into the tooth in its posterior half, reducing the lateral exposure of the talonid. In the present condition of the tooth no other reëntrants are discernible.

The P_4 is in a good state of preservation. The trigonid is stout, and in occlusal section the protomere area nearly approximates that of the paramere, but the lateral angle of the section is sharper than the median angle. The talonid, on the other hand, is small and shows slight lateral exposure in comparison with the trigonid—in general resembling the talonid of P_4 in *Gobiolagus tolmachovi* and *Gobiolagus andrewsi*—particularly the latter.

The M_1 shows a talonid approximating the trigonid in antero-posterior measurement, and the talonid contrasts further with that of P_4 in being considerably more transverse and in showing a greater lateral exposure; this comparison between P_4 and M_1, it will be noted, holds true in *Gobiolagus tolmachovi* and *Gobiolagus andrewsi* also. The trigonid of M_1 is somewhat more compressed antero-posteriorly on the lateral side than in *Gobiolagus andrewsi.*

The cheek teeth of this species show steeper lateral walls than those of *Gobiolagus andrewsi.* In P_4 and M_1 the trigonids have greater lateral extent than the talonids, although in M_1 the talonid shows a greater lateral extent relative to the trigonid, than in *Gobiolagus andrewsi.* In both teeth the trigonids jut medially beyond the talonids to some degree. The internal valley is not persistent and is not preserved in the teeth of this specimen.

A most interesting feature of P_4 and M_1 of this species and one not found in these teeth in *Gobiolagus tolmachovi, Gobiolagus* (?) *major* and *Gobiolagus andrewsi,* is shown on the internal wall of the crown of each. There is a reëntrant curve in the wall posterior to the internal reaches of the external valley. Within this vertical trough run two parallel grooves, with a delicate ridge between them. The origin of this ridge is not clear, in the absence of the internal valley, but it might represent a slight development of something in the way of a mesostyle. Some support for this hypothesis might be found in a specimen of *Desmatolagus robustus* in the Car-

negie Museum collection which shows a small tubercle in the exit of the internal valley of P_4. Such a tubercle might persist, with hypsodonty, as a ridge, defined by grooves anterior and posterior to it.

The anterior wall of the alveolus for M_2, as preserved in this specimen, is coated with a thick layer of cement.

Teilhard[1] has described a mandibular ramus which appears to represent this species; I am quoting his description for the benefit of other workers who may not have it at hand:

Cette mandibule, dont la face interne et les couronnes dentaires sont malheureusement trop altérées pour qu'on puisse fonder sur elle la description d'une espèce nouvelle, pourrait être confondue, à première vue, avec une mâchoire de *Desmatolagus robustus* dont elle a, à peu de chose près, la longeur dentaire (P_3–M_3 = 10 millimètres, au lieu de 11). Mais de cette espèce elle diffère, en réalité, par plusiers caractères importants:

a. D'abord, chez elle, la branche horizontale de la mandibule est notablement plus profonde (10, 5 au lieu de 9).

b. Ensuite, P_3 est à croissance absolument continue, et plus longue (dans le sens antéro-postérieur) que P_4.

c. Enfin, sur P_4, le talon, au lieu d'être au moins aussi long que sur M_1, est notablement plus court, moins détaché, plus arrondi que sur cette dent. A son tour, M_1 a un talon moins développé que M_2. M_3 parait relativement plus long, avec racines mieux séparées que sur les autres *Desmatolagus*.

Par la brièveté de sa P_4 et la longeur relative de sa P_3, la mandibule que nous venons de décrire diffère, non seulement de *Desmatolagus robustus*, mais de tous les *Desmatolagus* que nous avons énumérés plus haut. Elle mériterait donc peut-être la création d'un genre spécial. Son mauvais état de conservation et le fait que sa P_3 ne présente, comme elle des *Desmatolagus*, que deux lobes (ou colonnettes) externes, au lieu de trois (comme celle des *Lagomys* et des Léporidés), nous décident à ne pas lui donner, au moins provisoirement, de nom nouveau.

The generic position of *Gobiolagus* (?) *teilhardi* must remain in some doubt until better material representing the species is available; when such material is studied, the species may prove to belong to a distinct genus. It is a temptation to propose the phylogenetic series *Gobiolagus tolmachovi* → *Gobiolagus andrewsi* → *Gobiolagus* (?) *teilhardi:* which may prove to be such, but certain considerations make me hesitate in this case. For one thing, *Gobiolagus* (?) *teilhardi* has in common with the Ulan Gochu *Gobiolagus* (?) *major* a few characters (large size, heavy ramus, and disproportionately small incisor) which, although not usually given much phylogenetic weight, nevertheless are suggestive of relationship between these forms. It is true that *Gobiolagus* (?) *major* lags behind its contemporary *Gobiolagus andrewsi* in specialization, but my recent studies of species of *Desmatolagus* in the Hsanda Gol have shown me that in that genus the larger *Desmatolagus robustus* is persistently less specialized than the contemporary *Desmatolagus gobiensis;* it is possible that within the *Gobiolagus* group we have a somewhat similar situation, with greater specific disparity, in the Ulan Gochu.

[1] Teilhard de Chardin, P., 1926, Descriptions des Mammifères Tertiaires de Chine et de Mongolie, Annales de Pal., Tome XV, p. 26.

MEASUREMENTS

Gobiolagus (?) *teilhardi* Burke, A.M.N.H. No. 20236 (holotype)

	mm.
Inferior I, antero-posterior	2.3
Inferior I, transverse	1.8
P_3, antero-posterior at alveolus	2.0
P_3, transverse at alveolus	2.0
P_4, antero-posterior (occlusal surface)	2.0
P_4, transverse (occlusal surface)	2.7
M_1, antero-posterior (occlusal surface)	2.4
M_1, transverse (occlusal surface)	2.8
Length of inferior premolar series at alveoli	5.4
Depth ramus under M_1 (lingual side)	12.4
Width superior region of ramus below M_1	5.0
Width superior region of ramus below P_4	4.8
Width superior region of ramus below P_3	4.3

Desmatolaginae, new subfamily

Derivatives of *Shamolagus* paralleling the Megalaginae, but with generally less progressive cheek teeth and with terminal cheek teeth (particularly P_3) more reduced and simplified.

INCLUDED GENERA.—*Desmatolagus* and possibly *Amphilagus*.

RANGE.—Oligocene, Asia, ?Europe, and North America.

DESMATOLAGUS MATTHEW AND GRANGER

Desmatolagus vetustus, new species

Figures 7–8

HOLOTYPE.—A.M.N.H. No. 26089, a right mandibular ramus with complete dentition.

REFERRED SPECIMENS.—A.M.N.H. No. 26094, a left maxilla with P^{2-4}, M^{1-2}; A.M.N.H. No. 26095, a right maxilla with P^{3-4}, M^{1-2}; A.M.-

N.H. No. 26093, a left mandibular ramus with complete dentition; A.M.N.H. No. 26099, a right mandibular ramus with all cheek teeth and broken incisor; A.M.N.H. No. 26083, a left mandibular ramus with cheek teeth complete, incisor broken; A.M.N.H. No. 26081, part of right mandibular ramus with P_{3-4}, M_1; A.M.N.H. No. 26082, part of left mandibular ramus with P_4, M_{1-3}; A.M.N.H. No. 26080, damaged right mandibular ramus with shattered P_4, M_{1-2} and roots of P_3; A.M.N.H. No. 26090, a left mandibular ramus with P_4, M_{1-2}.

HORIZON.—Ulan Gochu, Lower Oligocene.

LOCALITIES.—Holotype, A.M.N.H. No. 26089, and referred specimens A.M.N.H. Nos. 26093, 26094, 26095, and 26090 from Jhama Obo, East Mesa, Shara Murun Region, Inner Mongolia; referred specimens A.M.N.H. Nos. 26080, 26081, 26082, 26083, and 26099 from Twin Obo, East Mesa, Shara Murun Region, Inner Mongolia. Central Asiatic Exped., 1928.

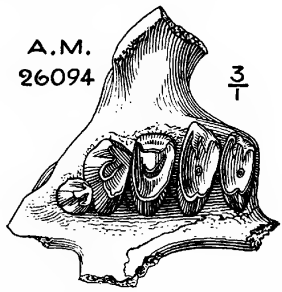

Fig. 7. *Desmatolagus vetustus* Burke, referred specimen. A.M.N.H. No. 26094. Ventral aspect of left maxillary with P^{2-4}, M^{1-2}, ×3.

DIAGNOSIS.—Distinguished from other species of *Desmatolagus* by: size (somewhat larger than *Desmatolagus gobiensis* but smaller than *Desmatolagus gazini*); lesser antero-posterior compression of cheek teeth; greatest width of maxillary tooth row usually at M^1, of mandibular tooth row usually at M_2; P^2 rotund, not attenuate, less reduced; P^3 not compressed at antero-posterior angle; P^4 without notch between lateral cusps; attenuation of P_3 not marked, trigonid lobe of P_3 with anterior reëntrant, but protoconid prominent; M_3^3 less reduced.

In addition to the holotype and several other mandibular rami, two maxillae are referred to this species. These specimens, A.M.N.H. Nos. 26094 and 26095, compare best in size with those of *Desmatolagus gobiensis* from the Hsanda Gol Oligocene, but are larger than the holotype maxilla of that species, and more robustly constructed. The Oreodon Beds Oligocene species *Desmatolagus gazini* is somewhat larger than the species under description, but its holotype maxilla, though considerably damaged, would appear to be nearer that of *Desmatolagus vetustus* in relative heaviness. So, too, are the maxillae of the larger species of *Desmatolagus* of which we know—those of *Desmatolagus dicei* and *Desmatolagus robustus*, both of the latter showing the heaviness on the external side in the antorbital region which distinguishes *Desmatolagus vetustus* from *Desmatolagus gobiensis*. Both of these maxillae referred to *Desmatolagus vetustus* preserve the suture between the maxilla and the malar; the latter bone dove-tails with the maxilla and extends forward above the posterior part of P^3. In lateral external view, the maxilla shows as a thin splint above the malar, but below the suture is more oblique and considerable of the maxilla is exposed. It is of interest that the suture is preserved in these specimens, in which the teeth are mature and well worn: I find the suture showing well in the holotype of *Desmatolagus dicei* also, and in that specimen the teeth are much worn. In all the specimens of *Desmatolagus gobiensis* and *Desmatolagus robustus* which I have examined, the suture is either obliterated entirely or in part.

The maxillary portion of the palatal bridge in *Desmatolagus vetustus* arises in advance of P^3, which is in contrast with the situation in *Desmatolagus gobiensis*, where this portion of the bridge arises posterior to the alveolus of P^3. However, in *Desmatolagus robustus*, which is the only other species represented by specimens preserving this region of the palate, the maxillary portion of the palatal bridge also extends farther anteriorly.

The P^2 of *Desmatolagus vetustus* is preserved in A.M.N.H. No. 26094. It is a relatively larger tooth than in *Desmatolagus gobiensis* generally, less attenuated, and swells more rapidly toward the base. In these respects it approaches to some extent the same tooth in *Desmatolagus robustus*, although P^2 of the latter is usually relatively smaller, and like that of *Desmatolagus gobiensis* shows a tendency toward flattening of the anterior face of the tooth and reduction of the paracone lobe.

P^3 in both maxillae of the species under

description lacks a protoloph, not even showing a short protoloph of the type found in the holotypes of *Desmatolagus dicei* and *Desmatolagus gazini*. It differs from P^3 of the latter forms also in showing a much more robust development at the postero-external angle, and in being more extended antero-externally, which gives it more of a triangular outline in occlusal view. However, neither of the North American species shows the compressed or pinched antero-external angle of P^3 which usually characterizes *Desmatolagus gobiensis* and which contrasts so strongly with the condition found in *Desmatolagus vetustus*. In general, the more triangular type of P^3 found in *Desmatolagus robustus* is more like that of *Desmatolagus vetustus* than the type of P^3 found in other species of *Desmatolagus*. The P^3 of *Desmatolagus robustus* also approaches that of *Desmatolagus vetustus* in failing to show marked reduction of the postero-external angle, but it differs from the latter, also from the American species and agrees with *Desmatolagus gobiensis*, in showing a better defined vertical groove on the anterior face in the region of the protocone.

P^4, M^1, and M^2 of the Hsanda Gol species of *Desmatolagus* show a tendency (most marked in *Desmatolagus gobiensis*) toward the development of a reëntrant outer border between the trigon and talon external cusps. This is shown to some extent in the molars of the earlier Oligocene forms, including *Desmatolagus vetustus* but I have not noted it in P^4 of the Lower Oligocene species.

Neither P^3 nor P^4 of *Desmatolagus vetustus* is as transverse, i.e., extends as far externally, as do those teeth in the maxilla of the American species of *Desmatolagus* and the forms from the Hsanda Gol. When the superior tooth row of *Desmatolagus vetustus* is viewed at the occlusal surface, the external outline does not approximate a smooth curve, but is staggered and jagged anterior to M^1. However, if one observes this outline of the maxillary tooth row in *Desmatolagus vetustus*, *Desmatolagus dicei*, and *Desmatolagus gazini*, *Desmatolagus robustus* and *Desmatolagus gobiensis* in the order named, he will observe that P^{3-4} gradually becomes more transverse on the external side, approximating each other and the molars, so that in the Hsanda Gol forms, this external outline of the tooth row, in occlusal view presents a fairly uniform curve from P^3 to M^3, best shown in *Desmatolagus gobiensis* which in this, as in most other respects, is more specialized than its contemporary *Desmatolagus robustus*.

This increase in transverse extent carries with it, in P^4 at least, an increase in size which is also observable in the series, so that, while we find P^4 in *Desmatolagus vetustus* a tooth a little smaller than, or approximating M^1 in size, in the Hsanda Gol forms it is as a rule definitely the larger tooth.

I find little in the pattern of P^4 of *Desmatolagus vetustus* which might serve as a basis for specific distinction. Even the ectoloph-like external wall occurs as a variation in *Desmatolagus gobiensis*. In the two maxillae referred to *Desmatolagus vetustus* the internal reëntrants are still preserved in P^3 and P^4, but, as in other species of *Desmatolagus* there is no trace of the enamel island such as we find in *Palaeolagus*, although the island is present in M^{1-2}. In this respect, as in many others, *Desmatolagus* resembles *Magalagus* and *Mytonolagus*.

The M^1 and M^2 of *Desmatolagus vetustus* appear to differ from the same teeth in later Oligocene forms, and notably from *Desmatologus gobiensis* in being less compressed antero-posteriorly, and in showing lesser delicacy and sharpness of the pattern elements. It is also worthy of note that in M^{1-2} of *Desmatolagus vetustus* the internal reaches of the external valleys have been obliterated by wear, although the enamel island still remains. This is in contrast to the condition found in *Desmatolagus gobiensis* where the inner reaches of the antero-external valley persist, together with the island, even after the external course of the valley has been obliterated.

M^2 of *Desmatolagus vetustus* does not show an unusually short postero-external crest of the type found in *Desmatolagus gazini*. However, as the penultimate cheek tooth, M^2 in these forms can be ex-

pected to show rather considerable variation, and I doubt whether this short crest will prove a constant specific character in *Desmatolagus gazini*.

Neither of the two maxillae referred to *Desmatolagus vetustus* preserves M^3, but the alveolus for this tooth is shown in both cases, and its size suggests that the tooth was less reduced than in later Oligocene forms.

While in point of size the mandible of *Desmatolagus gobiensis* comes nearest that of the species under description, although a little smaller, it is in full accord with the maxilla of that species in lacking the heaviness found in *Desmatolagus vetustus*. In this respect, again as was noted under

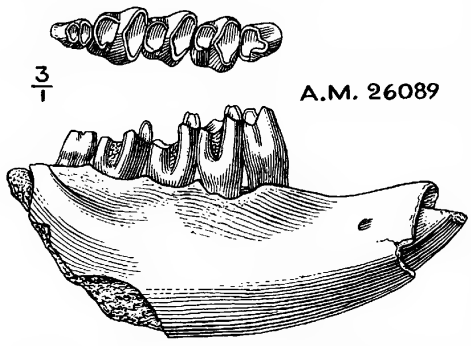

Fig. 8. *Desmatolagus vetustus* Burke, holotype, A.M.N.H. No. 26089. Lateral view of mandibular ramus and occlusal view of P_{3-4}, M_{1-3} right, ×3.

the description of the maxilla, *Desmatolagus vetustus* makes an approach to *Desmatolagus robustus* and *Desmatolagus dicei*. The diastema appears to be about the same as in the two Hsanda Gol species. In the holotype mandibular ramus of *Desmatolagus vetustus* the anterior mental foramen is located midway of the diastema, the posterior mental foramen beneath the talonid of P_4; in a paratype of *Desmatolagus gobiensis* the posterior mental foramen is somewhat, and the anterior mental foramen noticeably, posterior to these positions. Although there is considerable variation in regard to the placement of these foramina in both species, the tendency in *Desmatolagus gobiensis* seems to be in the direction of a more posterior location. Two posterior mental foramina sometimes occur in *Desmatolagus vetustus* as in *Desmatolagus gobiensis*. In *Desmatolagus robustus* the anterior and the posterior mental foramina sometimes occur even anterior to their position in the holotype of *Desmatolagus vetustus*. The ascending ramus arises at a much steeper angle in *Desmatolagus gobiensis* than it does in *Desmatolagus vetustus;* the species under description again approaching *Desmatolagus robustus* in this respect, for the ascending ramus of the larger Hsanda Gol species also arises at a lower angle than that of *Desmatolagus gobiensis*. A.M.N.H. No. 26083, referred to *Desmatolagus vetustus*, preserves enough of the dental foramen to show the latter as slit-like and extended nearly vertically, as in later species of *Desmatolagus*, rather than obliquely, as in *Shamolagus grangeri*. In the specimens of *Desmatolagus vetustus* at hand, the masseteric fossa is not well preserved except in A.M.N.H. No. 26083, which is a young specimen, but from what I can make out of it in the older specimens, it was not as deeply excavated as in the Hsanda Gol forms of *Desmatolagus*, and it did not have its antero-dorsal boundary as sharply defined. The present species is somewhat larger than *Shamolagus medius*, the Eocene form with which it compares best, and from which it appears to be derived. The Ulan Gochu species shows a little increase in depth and heaviness of the ramus anteriorly, but the principal differences of note are to be found in the cheek teeth.

The mandibular incisor of this species is trihedral in cross-section, with a flattened anterior face. It arises beneath M_1 and is larger than that of *Shamolagus medius*. It seems to present no salient characters distinguishing it from the lower incisors of other species of *Desmatolagus*.

The P_3 of *Desmatolagus vetustus* is a stout tooth, a crudely cylindrical peg, expanding somewhat toward the base anteriorly and laterally. There is a single external reëntrant which extends less than half the distance across the occlusal surface of the tooth in the holotype. In the holotype also the anterior face of this tooth is broadly concave on its lingual side

but the reëntrant thus indicated is somewhat less persistent than the external reentrant. This is the usual pattern shown in P_3 of mature specimens of *Desmatolagus vetustus;* no other reëntrants show at this stage of wear and the shaft is tri-lobed at the occlusal surface.

This, in its essentials, is the worn *Desmatolagus* P_3 pattern. I am strongly inclined to believe that it has not been derived from the P_3 pattern of *Shamolagus* without marked modification. There is a mandibular ramus of a young specimen of *Desmatolagus vetustus,* A.M.N.H. No. 26083, which preserves P_3 at an early stage of wear; in this specimen the broad anterior reëntrant is shown, as in the holotype, but posterior to it, on the lingual side and anterior to the external reëntrant is a third reëntrant, not as persistent as either of the former. This could represent either one of the two internal reëntrants of P_3 of *Shamolagus*—the antero-internal or the postero-internal, but I am interpreting it as the antero-internal because it resembles that reëntrant as it usually appears in P_3 of the *Duplicidentata,* because it arises in advance of the external reëntrant, and because the postero-internal reëntrant is least persistent in *Shamolagus* and might be expected, in view of the compression of the talonid found in *Desmatolagus,* to be eliminated from the crown surface.

If this interpretation is correct, however, we must conclude that the anterior lobe of P_3 of *Desmatolagus* is only homologous in part with that of P_3 of *Shamolagus:* to put it in another way, the trigonid lobe of *Shamolagus* is undivided—in *Desmatolagus* the trigonid lobe is divided by an anterior reëntrant corresponding to an anterior valley. There are indications that "molarization" of P_3 (sub-division of the trigonid) has been attained by most duplicidentates during the Oligocene, as shown in *Palaeolagus, Megalagus,* and *Titanomys,* even though in some cases it shows as little more than a flattening of the anterior face of the trigonid.

The modification of the trigonid in P_3 of *Desmatolagus vetustus* from the condition found in P_3 of *Shamolagus medius* has drawn the anterior wall of the external reentrant valley mediad, widening the latter valley and giving considerably more exposure of the lateral talonid wall in anterior view. The lateral side of the talonid is also more compressed antero-posteriorly than in P_3 of *Shamolagus medius* and its lateral wall is steeper.

The P_3 of *Desmatolagus robustus* shows less attenuation than that of *Desmatolagus gobiensis,* however, and the unworn pattern may resemble that of *Desmatolagus vetustus.*

A.M.N.H. No. 26080 shows this tooth to have been double-rooted, with the roots arranged antero-posteriorly.

The principal differences between P_3 of *Desmatolagus vetustus* and the same tooth of *Desmatolagus gobiensis* consist in greater attenuation of the tooth shaft in the Hsanda Gol species, which carries with it less marked expansion of the tooth toward the crown base, and steeper crown walls, particularly anteriorly and externally; some transverse compression of the anterior lobe and antero-posterior compression of the talonid—the latter exhibited in the sharp external talonid wall, the flattening of the posterior wall against P_4, and the antero-posterior reduction of the talonid on the internal side. This reduction of the talonid on the internal side seems to be due to a great extent to the continued widening and shallowing of the anterior reëntrant; the latter often appears more like a wide plane face, rather than a groove, on the antero-lingual side of P_3 of *Desmatolagus gobiensis.* Perhaps the most noticeable features of P_3 of *Desmatolagus gobiensis* in contrast with that tooth in *Desmatolagus vetustus* are the greater attenuation of the tooth in the Hsanda Gol species, and the wider groove or face at the antero-lingual angle.

Prevalent in many specimens of *Desmatolagus gobiensis* but not shown in any of the specimens of *Desmatolagus vetustus* at hand is the development of a tubercle at the base of the antero-internal reëntrant valley.

As might have been expected, considering other similarities in the two forms, the P_3 of *Desmatolagus robustus* makes a much closer approach to that of *Desmatolagus*

vetustus than does P_3 of *Desmatolagus gobiensis*. In fact, the only differences, outside of size, which appear to me as consistently distinguishing the two are shown in the greater attenuation of the tooth shaft, lesser expansion toward the base of the crown, and steeper walls; also the greater persistence of the external reëntrant, in *Desmatolagus robustus*.

The P_4 of *Desmatolagus vetustus* is a relatively larger tooth than that of *Shamolagus medius*. The tooth is less attenuate from the base to the crown surface on the external side; the external walls of the trigonid and the talonid are steeper; the trigonid is less swollen toward the base on the protomere side, the transition from crown to root is less abrupt, and the enamel has extended further down the trigonid root on the lateral side. The trigonid, laterally, no longer crowds the talonid toward the base of the crown to the extent that it did in *Shamolagus medius;* while the talonid shows more expansion toward the base on that side. Seen at the occlusal surface, the talonid is larger than in *Shamolagus medius* and sub-round in outline, not triangular as in *Shamolagus medius;* the trigonid is more compressed antero-posteriorly, particularly on the protomere side, its occlusal surface showing less of the pear-shaped outline. The external valley is wider.

When comparison is made with P_4 of *Desmatolagus gobiensis*, P_4 of *Desmatolagus vetustus* is seen to approximate that tooth in *Shamolagus* in the rotundity of the lateral side of its trigonid and its preservation of something of the pear-shaped trigonid occlusal section. The P_4 of *Desmatolagus gobiensis* is a more hypsodont tooth, with steeper walls and more angular occlusal sections; the trigonid is compressed antero-posteriorly and the talonid shows a triangular, rather than a sub-round occlusal section. Its reëntrant valleys are also narrower and less persistent, and the external valley is V-shaped. In regard to its "molarization" stage, the tooth probably makes its nearest approximation to *Desmatolagus dicei*. It is interesting that *Desmatolagus dicei* also shows the small P_4 (M_2 is the largest mandibular cheek tooth in that species). The greatest width of the mandibular tooth row is usually at M_2 in *Desmatolagus vetustus* also, although I have found one exception to this, A.M.-N.H. No. 26090, a mandibular ramus of a young individual showing the greatest width of the tooth row at P_4. In *Desmatolagus robustus* P_4 appears to be consistently the widest tooth.

A.M.N.H. No. 26080 indicates that this tooth was double-rooted.

One specimen, A.M.N.H. No. 26099, shows a P_4 which has revolved 90° in the ramus, with the trigonid medial in position and the talonid lateral. Judging from the wear on the tooth I think it must have functioned in this position during the animal's lifetime.

In general, in comparison with *Desmatolagus gobiensis*, many of the differences pointed out in the discussion of the fourth premolars of the two species hold true for the molars as well. The M_1 of *Desmatolagus vetustus* differs rather strikingly from the M_1 of *Shamolagus medius* in showing the sub-round, rather than triangular talonid occlusal section; the talonid is also reduced in size when compared with that of the latter species. But the molars of *Desmatolagus vetustus* still approximate the type found in *Shamolagus* in being relatively low-crowned with persistent internal valleys, whereas in *Desmatolagus gobiensis* the teeth are more hypsodont and the internal valleys less persistent. In the latter species, too, the molars have undergone more antero-posterior compression, the lateral protomere walls are more angular, the external valleys are V-shaped and the talonids are triangular, rather than sub-round in occlusal section. In the above assemblage of characters *Desmatolagus robustus* approximates *Desmatolagus vetustus* more nearly than *Desmatolagus gobiensis* does; it shows less antero-posterior compression of the molars and more persistent internal valleys. Nevertheless, in addition to greater size, the larger Hsanda Gol species shows the greatest width of mandibular tooth row at P_4 and greater reduction of M_3 than *Desmatolagus vetustus*. The M_3 is also reduced in *Desmatolagus dicei*, although the latter approaches

Desmatolagus vetustus in crown height and in having the greatest width of mandibular tooth row at M_2; it is, however, a much larger species.

The postero-internal reëntrant marking off the "third lobe" is shown in P_4 and M_1 in A.M.N.H. No. 26090 and in the same teeth in A.M.N.H. No. 26083. The M_3 of the latter specimen also shows two distinct cusps, one lateral, the other medial, on the talonid.

MEASUREMENTS

Desmatolagus vetustus Burke, A.M.N.H. No. 26089 (holotype)	mm.
Inferior I, antero-posterior	2.0
Inferior I, transverse	1.7
P_3 antero-posterior (occlusal surface)	1.2
P_3 transverse (occlusal surface)	1.6
P_4 antero-posterior (occlusal surface)	2.1
P_4 transverse (occlusal surface)	2.6
M_1 antero-posterior (occlusal surface)	2.1
M_1 transverse (occlusal surface)	2.2
M_2 antero-posterior (occlusal surface)	2.1
M_2 transverse (occlusal surface)	2.4
M_3 antero-posterior (occlusal surface)	1.2
M_3 transverse (occlusal surface)	1.2
Length of inferior premolar series at occlusal surface	3.1
Length of inferior premolar series at alveoli	3.7
Length of inferior molar series at occlusal surface	5.1
Length of inferior molar series at alveoli	6.0
Length mandibular tooth row at occlusal surface	8.4

A.M.N.H. No. 26094 (referred specimen)	
P^2 antero-posterior (occlusal surface)	0.9
P^2 transverse (external border to inner edge of occlusal surface)	1.2
P^2 transverse (external border to inner alveolar margin)	1.5
P^3 antero-posterior (occlusal surface)	1.4
P^3 transverse (external border to inner edge of occlusal surface)	2.6
P^3 transverse (external border to inner alveolar margin)	3.3
P^4 antero-posterior (occlusal surface)	2.1
P^4 transverse (external border to inner edge of occlusal surface)	3.1
P^4 transverse (external border to inner alveolar margin)	4.0
M^1 antero-posterior (occlusal surface)	2.1
M^1 transverse (external border to inner edge of occlusal surface)	3.6
M^1 transverse (external border to inner alveolar margin)	4.3
M^2 antero-posterior (occlusal surface)	1.7
M^2 transverse (external border to inner edge of occlusal surface)	2.8
M^2 transverse (external border to inner alveolar margin)	4.2
Length of superior premolar series (at occlusal surface)	4.3
Length of superior molar series (at occlusal surface) (est.)	4.0
Maxillary tooth row, alveolar measurement (est.)	9.5

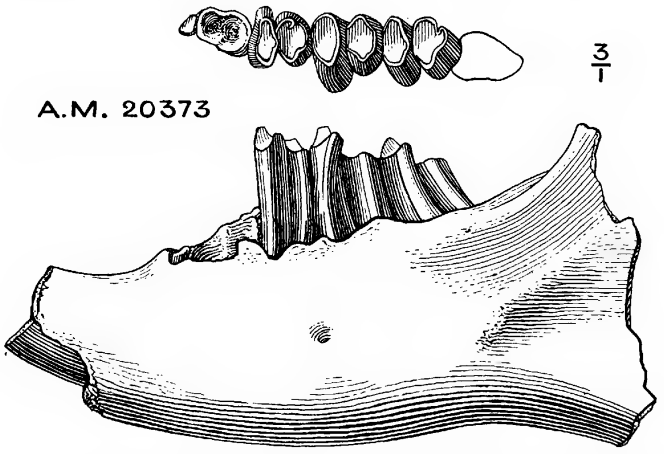

Fig. 9. *Desmatolagus ardynense* Burke, holotype, A.M.N.H. No. 20373. Lateral view of mandibular ramus and occlusal view of P_4, M_{1-2} left, ×3.

Desmatolagus ardynense, new species

Figure 9

Desmatolagus robustus MATTHEW AND GRANGER, 1925, Amer. Mus. Novit., No. 193, p. 7.

HOLOTYPE.—A.M.N.H. No. 20373, a left mandibular ramus with P_4, M_{1-2}, anterior root of DP_3, and broken incisor.

REFERRED SPECIMEN.—A.M.N.H. No. 20374, a right mandibular ramus with P_4, M_{1-2}.

HORIZON.—Ardyn Obo, Lower Oligocene.

LOCALITY.—Ardyn Obo, Mongolia. Central Asiatic Exped., 1923.

DIAGNOSIS.—About the size of *Desmatolagus robustus* but with smaller P_4; cheek teeth less compressed antero-posteriorly. M_1 the largest mandibular cheek tooth.

In general proportions (size, relative heaviness, diastema, and depth of ramus) the mandibular ramus of this species would apparently fall within the range of *Desmatolagus robustus*. The ramus narrows transversely anterior to M_1, however, in the holotype, which is of a young individual; in the referred specimen, from an old individual, the narrowing at this place is slighter. In *Desmatolagus robustus* the narrowing of the ramus seems usually to occur anterior to P_4. The anterior mental foramen is carried forward and occurs at the incisive region of the diastema in the young holotype specimen. The posterior mental foramen lies between and beneath P_4 and M_1 (in A.M.N.H. No. 20374 just beneath the talonid of P_4). The slope of the ascending ramus is not as steep as in *Desmatolagus robustus* and *Desmatolagus dicei*. The masseteric fossa is very shallow in the young holotype specimen, but shows moderate development in A.M.N.H. No. 20374. The scar is not as distinct as in *Desmatolagus robustus* and *Desmatolagus dicei*, but in A.M.N.H. No. 20374 the tubercle anterior to the scar is a little reminiscent of that in *Shamolagus*. The slit of the dental foramen is more oblique than in *Desmatolagus robustus*.

The incisor of A.M.N.H. No. 20373 seems less angular in cross-section than that of *Desmatolagus robustus* but this may be a character dependent upon the stage of growth. The incisive swelling, however, indicates that the incisor extended posteriorly beneath M_1, whereas in *Desmatolagus robustus* the incisor does not appear to extend posterior to P_4.

P_3 is not preserved, but its alveolus suggests that it was larger than P_3 of *Desmatolagus robustus*. Anterior to the alveolus appears the base of the root of DP_3; this is the "minute vestigial stump of a tooth" mentioned by Matthew and Granger.[1] This is plainly the remnant of the anterior root of the milk tooth, not a vestige of P_2.

The cheek teeth, in general, show less antero-posterior compression than those of *Desmatolagus robutus*.

The P_4 is relatively a smaller tooth than in *Desmatolagus dicei* and much smaller than in *Desmatolagus robustus*, where P_4 is "molariform" and as large as, or larger than M_1. P_4 in the holotype preserves the postero-internal reëntrant marking off the "third lobe."

The M_1 is the largest and most transverse of the mandibular cheek teeth. This contrasts with the situation in *Desmatolagus robustus* where M_1 is sometimes smaller than P_4 or M_2. In *Desmatolagus dicei* M_2 is the largest of the mandibular cheek teeth and the most transverse.

The M_2 in the holotype of *Desmatolagus ardynense* preserves the postero-internal reëntrant.

The alveolus for M_3 suggests that the tooth was larger than in *Desmatolagus dicei* or *Desmatolagus robustus*.

Desmatolagus ardynense is apparently little advanced beyond *Desmatolagus dicei* in specialization but is definitely less specialized than *Desmatolagus robustus;* it probably gave rise to the Hsanda Gol species.

MEASUREMENTS

Desmatolagus ardynense Burke, A.M.N.H. No. 20373 (holotype)

	mm.
P_3 alveolus, antero-posterior	2.6
P_3 alveolus, transverse	2.0
P_4 antero-posterior (occlusal surface)	2.2
P_4 transverse (occlusal surface)	2.0
M_1 antero-posterior (occlusal surface)	2.8
M_1 transverse (occlusal surface)	2.4
M_2 antero-posterior (occlusal surface)	2.9
M_2 transverse (occlusal surface)	2.4
M_3 alveolus, antero-posterior	2.2
M_3 alveolus, transverse	1.8
Length of inferior premolars at alveoli (app.)	5.5
Length of inferior molars at alveoli (app.)	8.5
Length mandibular tooth row at alveoli (app.)	14.2
Depth ramus under M_1 (lingual side)	9.7

[1] Matthew, W. D., and Granger, Walter, 1925, "New Creodonts and Rodents from the Ardyn Obo Formation of Mongolia." Amer. Mus. Novit., No. 193, p. 7.

Width superior region of ramus below M_2	4.7	Width superior region of ramus below P_3	3.6
Width superior region of ramus below M_1	4.9	Inferior I, antero-posterior	2.4
Width superior region of ramus below P_4	4.3	Inferior I, transverse	2.0

SUMMARY

There are now represented, in the Upper Eocene, three genera of Leporidae—*Mytonolagus* in North America, *Shamolagus*, and *Gobiolagus* in Asia. *Gobiolagus* is also found in the Lower Oligocene of Mongolia. These genera have in common certain features of the cheek teeth—presence of roots, general pattern, and molar-premolar proportions, plus an undivided trigonid lobe of P_3—which in combination are not found in later Leporidae. For this reason I have grouped the three genera in a common subfamily, the Mytonolaginae. Since the characters delimiting the Mytonolaginae will probably apply to an Upper Eocene and Eocene–Oligocene transition stage in the evolution of the Leporidae generally, the group will likely prove to include the stem stock of all later Leporidae.

The genus *Shamolagus* approximates the North American *Mytonolagus* in many respects, but differs from the latter mainly in showing more brachyodont anterior cheek teeth and a characteristic construction of the trigonids. The exceptionally large M_3 of *Shamolagus grangeri* will probably not be found in *Shamolagus medius* from the Ulan Shireh Beds, which are apparently older than the Myton Member of the Uinta Eocene in which *Mytonolagus petersoni* is found, and the smaller M_3 which characterizes the American Upper Eocene species will probably be approximated in *Shamolagus medius* which is derived from the Shara Murun Eocene, a geologically younger formation than the Ulan Shireh.

In P_3 of the holotype of *Shamolagus medius* we find P_3 preserving its full complement of reëntrants; the tooth in this specimen demonstrates that in that genus the trigonid lobe of P_3 is without grooves or reëntrants.

Contemporaneous with *Shamolagus medius* in the Shara Murun is *Gobiolagus tolmachovi*, representing the second genus of the Leporidae in the Mongolian Upper Eocene. *Gobiolagus* differs from *Shamolagus* and *Mytonolagus* in showing marked unilateral hypsodonty and a reduced P_4 characteristic of the genus.

In the next higher horizon recognized in Mongolia, the Ulan Gochu Lower Oligocene, *Gobiolagus andrewsi* appears to be an immediate descendant of *Gobiolagus tolmachovi*. Fortunately one specimen of this species in the present collection shows P_3 in an early stage of wear, and agrees with the holotype of *Gobiolagus tolmachovi* (in which P_3 is worn, however) in showing the trigonid lobe to be without grooves or reëntrants.

In the Ulan Gochu Lower Oligocene there occurs a large and aberrant species, *Gobiolagus* (?) *major* which combines cheek teeth in general much like those of *Shamolagus* and *Desmatolagus* with a P_4 of the *Gobiolagus* type. The true affinities of this form remain to be demonstrated; the P_3 is lacking in the unique holotypic specimen.

Before entering into a discussion of a third Ulan Gochu form, I think it best to point out the evolutionary lines present in the Mytonolaginae. As we have seen, the unilaterally hypsodont *Gobiolagus* is already represented by a sequence of two species and possibly by another but aberrant form. In the North American Upper Eocene occurs *Mytonolagus*, a form somewhat intermediate between *Shamolagus* and *Gobiolagus* in its specialization. *Shamolagus*, in the Mongolian Eocene, is represented by two species. So far, these three genera conform to the Mytonolaginae as defined, but in their later specializations these evolutionary lines all appear to diverge too widely to be retained in the stem subfamily. *Mytonolagus*, for example, appears to be allied with the North American Oligocene *Megalagus*. *Gobiolagus* is related to an advanced species in the Hsanda Gol Upper Eocene. *Shamolagus* leads up

to *Desmatolagus*. To trace the later evolution of these stocks, already represented in the Megalaginae, the all-inclusive family term "Leporidae" is not adequate.

In an attempt to cope with this difficulty I propose to use subfamily names rather freely, an action opposed to my former practice, since I feel that taxonomic prefixes are often the prelude to taxonomic confusion. But the subfamily is already established as a major taxonomic unit in the Leporidae and I am trying to make the most of it.

The term Palaeolaginae, at least to the extent that it includes the species of *Palaeolagus*, is an extremely convenient one. I would not extend it, as Wood[1] has recently proposed, for by doing so, the utility of the term is lost; it must be remembered that the phyla of Oligocene Leporidae can be established on more characters than the pattern of P_3 alone. I have found no transitions between *Palaeolagus* and *Megalagus* in the Oligocene; the two generic lines seem quite distinct. For this reason I propose to utilize Walker's term, Megalaginae, to characterize the forms included in this genus, rather than my previous clumsy term of "turgidus group." Dice's term Archeolaginae might be extended to cover these forms, but it seems to me that the use of subfamily names to mark off evolutionary stages in the phyla of Leporidae also has its advantages—and gives rise to fewer wild surmises. The term Megalaginae might well be restricted to the Oligocene representatives of the *Megalagus* phylum which have rooted cheek teeth, among other characters, to distinguish them from later Leporidae.

For the *Desmatolagus* phylum, I am proposing a new subfamily, the Desmatolaginae, characterized by persistently unprogressive dentition and a tendency toward reduction and simplification of the terminal cheek teeth. The first representative of *Desmatolagus* is *Desmatolagus vetustus*, found in the Ulan Gochu Lower Oligocene of Mongolia. The form is the most primitive and generalized of the genus, but is advanced beyond the Mytonolaginae in a very important respect; the anterior lobe of the trigonid of P_3 is divided by a broad anterior reëntrant. From this species it is a fair conclusion that the anterior (or antero-lingual) reëntrant of later species of *Desmatolagus* does not correspond to the main lingual reëntrant valley, as might be supposed at first glance.

From a higher Lower Oligocene horizon than the Ulan Gochu, the Ardyn Obo, comes the second species of *Desmatolagus* described in the present paper—*Desmatolagus ardynense*. This large species is close to the Hsanda Gol form *Desmatolagus robustus* in specialization and is evidently ancestral to the latter.

In Asia the record of *Desmatolagus* is incomplete from the Ardyn Obo to the Upper Oligocene, but in North America *Desmatolagus dicei* in the Lower Oligocene and *Desmatolagus gazini* in the Middle Oligocene show increasing specialization of the genus. The record is completed in Asia in the Hsanda Gol Upper Oligocene where the genus culminates in species of the type of *Desmatolagus robustus* and *Desmatolagus gobiensis*.

Size and tooth pattern resemblances between *Desmatolagus vetustus* and *Desmatolagus gobiensis* suggest that there may be at least two evolutionary lines within the genus, the one represented by these smaller forms, more precocious in specialization, the other composed of larger, more conservative species including *Desmatolagus ardynense*, *Desmatolagus dicei*, and *Desmatolagus robustus*. The relationship of *Desmatolagus gazini* to these groups is not clear, although it appears to belong with the latter association.

After the Ulan Gochu Lower Oligocene, the record of the *Gobiolagus* stock is blank until we come to the Hsanda Gol Upper Oligocene. Here there occurs a large species, well specialized but with the characteristic reduced P_4 of the *Gobiolagus* stock. This form, *Gobiolagus* (?) *teilhardi*, may well represent a new genus, and when known from more complete material will probably be excluded from the Mytonolaginae by virtue of advanced specializa-

[1] Wood, Albert, 1940, "Lagomorpha," Trans. Amer. Phil. Soc., New Series, XXVIII, Part III, p. 276.

tion. While there is abundant time for this large species to have evolved from the small and more typical species *Gobiolagus andrewsi* of the Ulan Gochu, it is suggested that *Gobiolagus* (?) *teilhardi* might have descended from the aberrant *Gobiolagus* (?) *major* which also occurs in the Ulan Gochu and which tends toward *Gobiolagus* (?) *teilhardi* in size, heaviness of mandibular ramus, and in incisor reduction.

I fail to find any close relationship between these Mongolian genera and the genus *Sinolagomys* of Bohlin[1] from Western Kansu. *Sinolagomys* presents an interesting combination of characters, as Bohlin has described and figured it, including a wide internal reëntrant valley in the superior cheek teeth, the prevailing direction of which appears to be antero-lateral. The mandibular molars show a deep channel extending down the lateral side of the anterior face of the trigonid and a persistent internal reëntrant; in the mandibular tooth row the molar talonids tend to extend medial to the trigonids posterior to them. Bohlin apparently could not derive *Sinolagomys* from *Desmatolagus* (its contemporary) but suggested that the two forms had a common ancestry. However, the basic pattern of *Desmatolagus* is already present in *Shamolagus*, its Eocene ancestor; while these latter genera are relatively unprogressive and preserve various "primitive" duplicidentate characters, there seems little possibility that either might have given rise to *Sinolagomys*. *Gobiolagus*, a more progressive Mongolian genus, approximates even more decidedly the pattern of the modern Leporidae than *Shamolagus* and *Desmatolagus*, and likewise seems removed from possible ancestry of *Sinolagomys*.

In a previous paper[2] I have pointed out that the difference between the cheek teeth of the Ochotonidae and the Leporidae would seem to be chiefly a matter of pattern torsion; the two families appear to represent the extremes of divergent pattern trends. The derivation of the tooth pattern of the Ochotonidae from that of the Leporidae, while often inferred, remains to be demonstrated.

[1] Bohlin, Birger, 1937, "Oberoligozäne Säugetiere aus dem Shargaltein-Tal (Western Kansu)," Palaeontologia Sinica, New Series C, No. 3, Whole Series No. 107, pp. 7–66, Pls. I–II, 136 figs.

[2] Burke, J. J., 1936, "*Ardynomys* and *Desmatolagus* in the North American Oligocene," Ann. Car. Mus., XXV, pp. 152–153.